

## Anatomy and Affinities of Permineralized *Picea* Leaves from the Late Middle Miocene of Shimokawa Group, Hokkaido, Japan

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A new species of permineralized *Picea* leaf, *Picea nakauchii* sp. nov., from the late Middle Miocene of Shimokawa Town, Kamikawa-gun, Hokkaido Japan, is described as the first report of permineralized coniferous leaves from the Tertiary of Japan. The characteristics of the leaf form and vascular bundle of *P. nakauchii* resemble those of subsection *Picea* species. The small resin canals unique to *P. nakauchii* resemble *P. koyamai* and *P. shirasawae* now indigenous to central Honshu.

### Introduction

Studies on permineralized plants from the Tertiary of Japan have been limited to petrified woods. As far as we know, there is no work on leaves, cones, fern stipes and rhizomes and fructification. In 1987, 1988 and 1990, H. and M. Nishida and T. Ohsawa collected several lignite nodules from the Tertiary sediments of Shimokawa Town, Hokkaido, under the guidance of Mr. Isekichi Nakauchi who had collected permineralized *Osmunda* rhizomes from the same locality and horizon. These nodules contain numerous permineralized plants, cones, needles, fern pinnae, fern stipes, fern rhizomes, and other plant fragments as well as petrified woods. Here, we describe a new species of permineralized *Picea* leaf as a first report on the permineralized plants in these lignite nodules.

### Materials and Methods

Lignite nodules #870109, #882105, #903000, #903001, #903005 containing many leaves of *Picea*

(Fig. 2A) were collected by H. and M. Nishida and T. Ohsawa in 1987, 1988 and 1990 from the riverbed of the Rubeno-sawa, a small branch of the River Sanru, Shimokawa Town, Kawakami-gun, Hokkaido (Fig. 1).

The nodules were collected from the thick calcedonic quartz beds belonging to the Mosanru Formation of the lowermost Shimokawa Group. The age is late Middle Miocene (personal communication of H. Nishida). A detailed of geology of this area will be reported by H. Nishida. All micropreparations were made by the cellulose acetate peel technique (Joy *et al.* 1956) using 25% hydrofluoric acid as an etching reagent. Type specimens are deposited in the Laboratory of Phylogenetic Botany, Faculty of Science, Chiba University. For comparison with the fossil specimens, we collected nine species of modern *Picea*, and made leaf sections (Table 1). All the collected modern species have quadrangular leaves similar to the fossil specimens. Leaves of juvenile

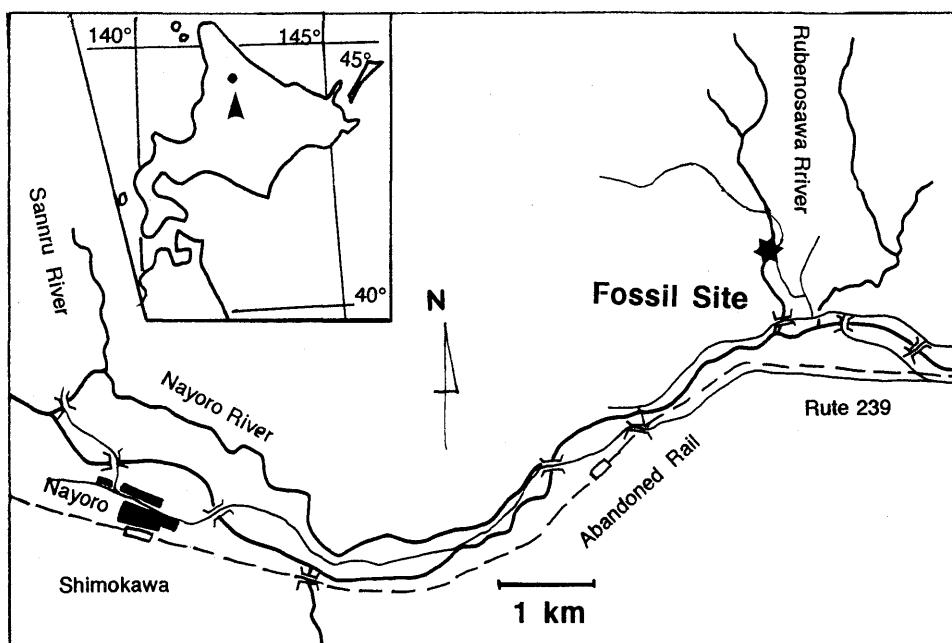


Fig. 1. Map of fossil locality.

plants of modern species, except *P. glehnii*, were collected from plants cultivated at the Tama Forest Science Garden, Forestry and Forest Products Research Institute, and at the Botanical Garden, Faculty of Science, University of Tokyo, and at Mt. Yatsugatake. Leaves from native and reproductive plants of *P. glehnii*, *P. koyamai*, *P. maximoxiczii*, *P. shirasawae*, and *P. torano* were examined from specimens collected by Y. Hayashi, A. Momohara, S. Ohsawa, T. Nirei, and S. Watari.

## Results

Systematic treatment  
Order Coniferales  
Family Pinaceae Lindley  
Genus *Picea* Dietr.  
Section *Picea* (Dietr.) Farjon  
Subsection *Picea* (Dietr.) Farjon  
Species *Picea nakauchii* sp. nov.  
Diagnosis. Needle leaf quadrangular, obtrullate to widely obtrullate outline in cross section; am-

phostomate with stomatal lines on four faces. Hypodermis usually single layered, rarely two or three layered at abaxial ridge and around resin canal. Endodermis well discernible, circular in cross section. Palisade tissue scarcely discernible. Resin canals small, marginal, located on abaxial side of lateral ridges. Transfusion tissue in pericycle. A single median vascular bundle divided into two parts by a narrow ray. Phloem fiber composed of single mass of thick-walled fibers.

Type and deposition. Specimen #870109 and its micropreparations (holotype), #882105, #903000, #903001, #903005, housed in Laboratory of Phylogenetic Botany, Faculty of Science, Chiba University.

Locality. Rivulet Rubeno-sawa, a branch of River Sanru, Shimokawa Town, Kawakami-gun, Hokkaido, Japan.

Horizon and Age. Mosanru Formation, lowermost Shimokawa Group, late Middle Miocene.

Etymology. Species epithet *nakauchii* is dedicated

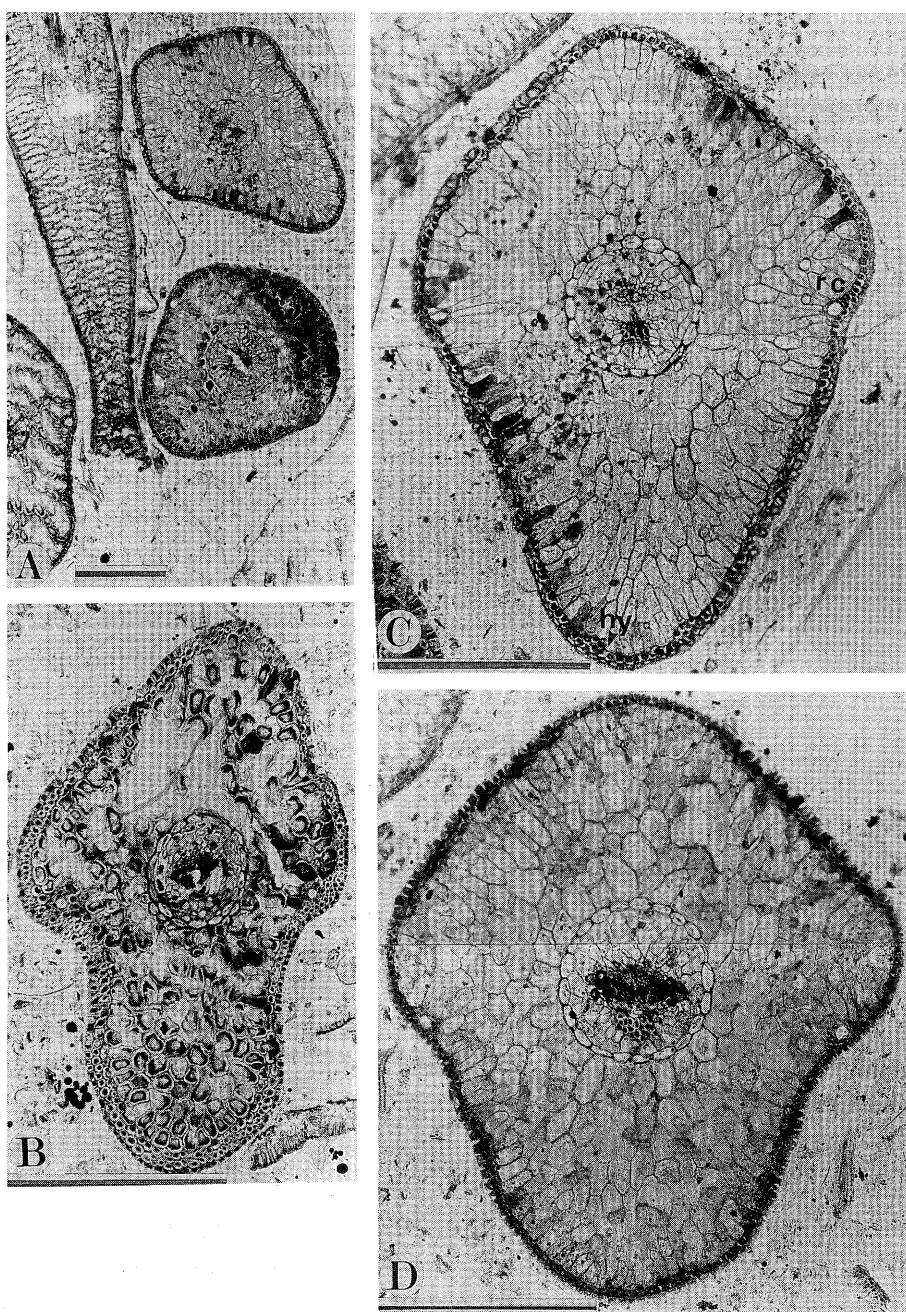


Fig. 2. *Picea nakauchii* sp. nov. A: Section from lignite nodule #870109. Note many leaves embedded in nodule. B: Cross section of leaf near base. Specimen #870109D. C: Cross section of leaf in obtusate outline. Specimen #870109A. D: Cross section of leaf in widely obtusate outline. Specimen #870109B. All bars = 0.5 mm.

Table 1. List of extant *Picea* species used in comparison

Species	Locality	Collector
<i>P. abies</i>	Kamakura, Kanagawa	Watari
<i>P. alcoquiana</i>	Asakawa, Tokyo	Matsumoto and T. Ohsawa
<i>P. glehnii</i>	Saghalin	Watari
<i>P. koyamai</i>	Asakawa, Tokyo	Matsumoto and T. Ohsawa
	Mt. Yatsugatake, Nagano	Hayashi
<i>P. maximowiczii</i>	Bot. Garden, Univ. Tokyo	Matsumoto and T. Ohsawa
	Mt. Yatsugatake, Nagano	Momohara, S. Ohsawa and T. Nirei
<i>P. pungens</i>	Asakawa, Tokyo	Matsumoto and T. Ohsawa
<i>P. shirasawae</i>	Asakawa, Tokyo	Matsumoto and T. Ohsawa
	Mt. Yatsugatake, Nagano	Hayashi
	Mt. Yatsugatake, Nagano	Momohara, S. Ohsawa and T. Nirei
<i>P. smithiana</i>	Asakawa, Tokyo	Matsumoto and T. Ohsawa
<i>P. torano</i>	Mt. Yatsugatake, Nagano	Momohara, S. Ohsawa and T. Nirei

to Isekichi Nakauchi, Shimokawa Town, who discovered the fossil locality.

**Description.** Since all specimens are embedded in lignite nodules, we can not examine the external morphology of the needles to measure their exact length. Small needle leaf 1.0–2.0 mm in diameter, obtrullate to widely obtrullate in outline in cross section (Figs. 2A, B, C, D). Various shapes ranging from longitudinally lengthened (0.5–1.0×1.0–1.8 mm in height and width, 60%) to laterally lengthened (1.2–1.5×1.5–2.0 mm in height and width, 25%), and right obtrullate (0.7–1.5×0.8–1.5 mm in diameter, 15%). Laterally-lengthened samples generally larger than longitudinally-lengthened samples in whole dimension.

Epidermis composed of only single layer of roundish square cells, 7.5–10  $\mu\text{m}$ ×10–12.5  $\mu\text{m}$  in dimension in transverse section (Figs. 3A, B). Walls 2.0  $\mu\text{m}$  in thickness.

Hypodermis composed mostly of one cell layer, sometimes two or three layers at abaxial ridge, and two layers near resin canals (Figs. 3B, E, G, 4A).

Hypodermal cells equal in form and size, slightly square, 8–10  $\mu\text{m}$ ×10–13  $\mu\text{m}$  in dimension, and compactly arranged inside epidermis. Walls of hypodermal cells thicker than walls of epidermis, and 4–7  $\mu\text{m}$

in thickness. Cells well preserved and mostly occluded with black substance. In basal section of leaf, wide part of hypodermis from abaxial ridge to both lateral resin canals becomes two layers (Figs. 2B, 3E), but is single layer at adaxial ridge (Fig. 3D).

Needles amphistomatic, bearing slightly-sunken stomata. One to three stomata examined on each face in cross section (Fig. 4A). Stomata probably arranged in three or more lines on each face.

Mesophyll consisting of palisade and spongy tissues, 4–8 cells thick in total; thicker on abaxial side than adaxial side (Figs. 2C, D, 4A). Palisade tissue slightly discernible and consisting of cells with elongated angular outlines, 50–150  $\mu\text{m}$ ×20–50  $\mu\text{m}$  in dimension, with thin walls 1.5–2.0  $\mu\text{m}$  in thickness. Palisade touching inside of hypodermis and composed chiefly of one layer of cells, but becoming up to two layers at adaxial ridge and up to three at abaxial ridge. Spongy tissue touching inside of palisade tissue composed of three to six layers of large roundish cells 30–50  $\mu\text{m}$ ×50–100  $\mu\text{m}$  in dimension, with walls 1.5–2.5  $\mu\text{m}$  in thickness. Thicker on abaxial side (four to six cells) than adaxial side (three to four cells). Cells more rounded in outline towards vascular bundle. Intercellular spaces are not apparent.

Resin canals very small, 20–35  $\mu\text{m}$  in diameter

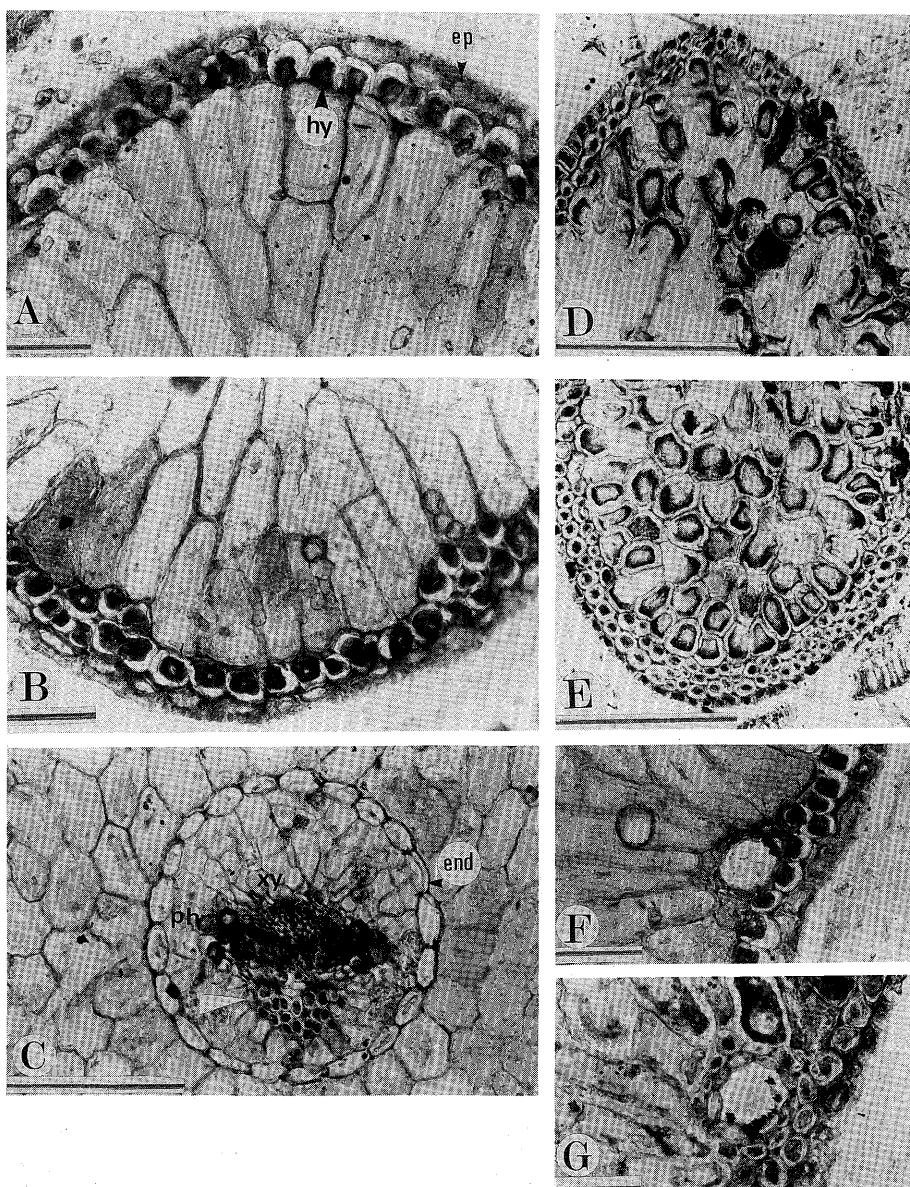


Fig. 3. *Picea nakauchii* sp. nov. A: Enlargement of epidermis (ep) and hypodermis (hy) of adaxial ridge of specimen #870109A. Bar = 50  $\mu\text{m}$ . B: Enlargement of epidermis and hypodermis of abaxial ridge of specimen #870109A showing partially two-layered hypodermis (arrows). Bar = 50  $\mu\text{m}$ . C: Enlargement of vascular bundle encircled by endodermis (end). Note single mass of phloem fibers. Specimen #870109B. Bar = 200  $\mu\text{m}$ . D: Enlargement of epidermis and hypodermis of adaxial ridge of specimen #870109D showing single-layered hypodermis. Bar = 200  $\mu\text{m}$ . E: Enlargement of epidermis and hypodermis of abaxial ridge of specimen #870109D showing two-layered hypodermis. Bar = 200  $\mu\text{m}$ . F: Enlargement around resin canal showing two-layered hypodermis. Specimen #870109A. Bar = 50  $\mu\text{m}$ . G: Enlargement around resin canal encircled by thick-walled cells. Specimen #870109B. Bar = 50  $\mu\text{m}$ .

(Figs. 3F, G). Usually two, rarely one or no canals, are examined in cross sections (Figs. 2B, C, D). Resin canals located just inside hypodermis and on both abaxial faces near lateral ridge. Canals encircled by 6–10 epithelial cells. Epithelial cells thin-walled with thin spindle-like outline in cross section (Fig. 3G). Sometimes inconspicuous because of narrow cell size (Fig. 3F). Outside of epithelial cells encircled by 6–10 sclerenchyma cells circular in cross section, 5–6  $\mu\text{m} \times 8\text{--}12 \mu\text{m}$  in dimension with walls 1.5–2.0  $\mu\text{m}$  thick (Figs. 3F, G).

Single vascular bundle running in central area of needle (Figs. 2B, C, D, 4A). Bundle completely encircled by well-differentiated endodermis consisting of 15–24, usually 17–21, cells (Figs. 3C, 4). Bundles elliptical or elongated elliptical in cross sec-

tion, 22–35  $\mu\text{m} \times 55\text{--}70 \mu\text{m}$  in dimension, with walls 1.5–2.5  $\mu\text{m}$  thick. Endodermis 260–380  $\mu\text{m}$  in diameter and becoming larger in relation to needle dimension. Pericycle consisting of 3–4 layers of parenchymatous cells, roundish polygonal in outline, 15–30  $\mu\text{m} \times 15\text{--}40 \mu\text{m}$  in dimension, with walls 1.5–2.5  $\mu\text{m}$  in thickness (Figs. 3C, 4B). Transfusion cells bearing bordered pits scattered in pericycle, although somewhat unclear because of poor preservation. Xylem consisting of tracheids, small circular or elliptical in outline, 5–7  $\mu\text{m} \times 5\text{--}8 \mu\text{m}$  in diameter and arranged in 9–12 rows and 4–5 layers, located in adaxial part of vascular bundle (Figs. 3C, 4B). Protoxylem not discernible. Phloem consisting of rectangular cells in cross section (Fig. 3C), but usually decayed and not preserved. Xylem and phloem divided into two by

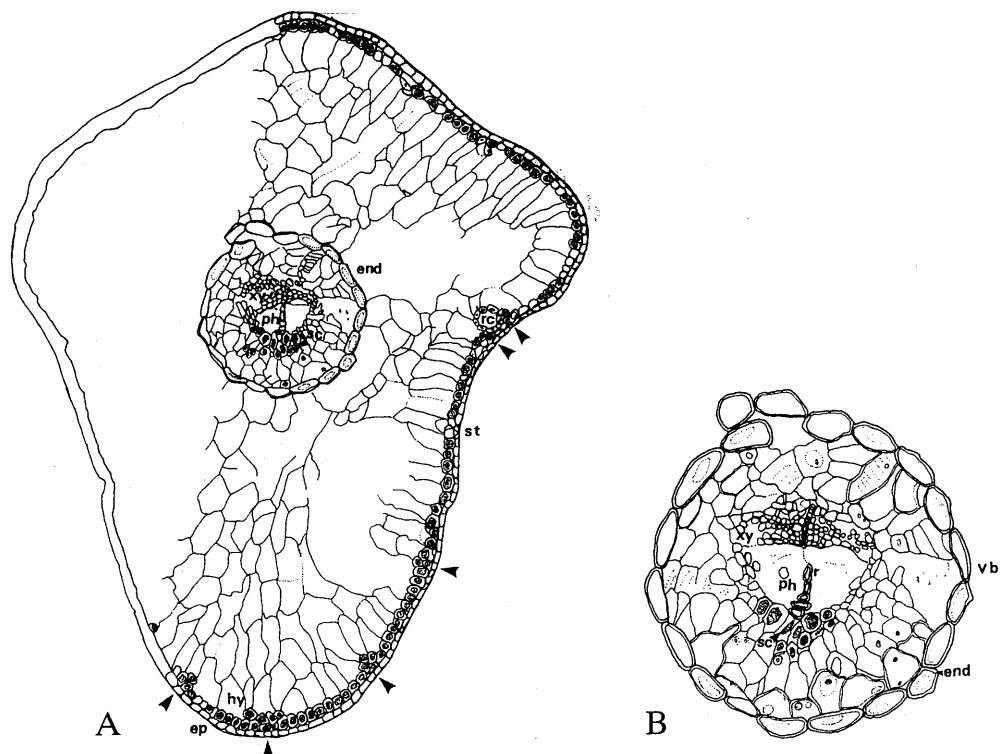


Fig. 4. A: Illustrated transverse section of *Picea nakauchii* sp. nov. B: Enlargement of vascular bundle in A. end, endodermis; ep, epidermis; hy, hypodermis; rc, resin canal; ph, phloem; sc, sclerenchyma; st, stomata; vb, vascular bundle; xy, xylem. Arrows, partially two layered hypodermis.

medullary uniseriate ray (Figs. 3C, 4). Single mass of phloem fibers, 4–5 cells in width and 1–3 cells in thickness discernible on abaxial side of phloem (Figs. 3C, 4B). Each fiber polygonal in outline, 15–22.5  $\mu\text{m} \times 7.5\text{--}15 \mu\text{m}$  in diameter, with walls 3.8–7.5  $\mu\text{m}$  in thickness.

### Affinity and Discussion

Comparison with pinaceous genera. As described above, *Picea nakauchii* is characterized by an obtrullate outline in cross section, amphistomatic leaves with several lines of stomata on each face, single small resin canal touching the hypodermis of both abaxial faces near the lateral ridges, a single median vascular bundle divided into two parts by a medullary ray, mesophyll that is scarcely differentiated into palisade and spongy tissues, a general single-layered hypodermis except for the abaxial ridge and parts near resin canals where a two-or-three layered hypodermis is seen, and a single mass of two or three layers of fibers on the abaxial side of the phloem.

The leaf form and two resin canals are characteristic of some genera of the Pinaceae. Of these genera, *Cedrus*, *Larix*, and *Picea* have the quadrangular outline in cross section (Farjon 1990). However, our specimens are distinguished from *Larix* which has a discontinuous hypodermis restricted to each ridge and resin canals in just lateral ridges (Farjon 1990). Our specimens also differ from *Cedrus* which has two separate vascular bundles. Thus our fossil specimens are thought to belong to *Picea*.

Evaluation of characters of modern *Picea* leaf. Before discussing the affinity of *P. nakauchii*, it is necessary to evaluate the value of certain features of the leaf in indicating the relationships of fossil leaves with modern species. Two forms of the outline in cross section are examined in the fossil specimen; longitudinally-lengthened and laterally-lengthened forms. In leaves of living plants, this form is highly variable (Schmidt 1989), and changes from a longitu-

dinally-lengthened form to a laterally-lengthened form as the plants grow up. Width is also narrower in the basal part. The frequency of two-layered hypodermis increases larger in reproductive plant. However, although the two-layered part is restricted to the abaxial ridge in leaves of reproductive *P. glehnii*, and although it is restricted to the abaxial ridge and parts around resin canals in leaves of reproductive *P. koyamai* and *P. shirasawae*, it appears in both the abaxial and adaxial ridges in leaves of juvenile *P. pungens*, *P. abies*, and *P. torano*. The diameter of resin canals, number of epithelial cells, number of fibers on the abaxial side of phloem, number of endodermis cells, and endodermis diameter increase as plants grow up. The size of these features in juvenile plants can be considered the lowest limit.

Comparison with modern *Picea*. Recently, Farjon (1990) improved the classification of Schmidt (1988), and classified *Picea* into two sections: *Picea* and *Casicta*, from the features of the seed cone. Each section is split into two subsections based on leaf form: subsections *Omorikae* and *Picea* in section *Picea*, and subsections *Sitchensis* and *Pungentes* in section *Casicta*. We follow this classification. Subsection *Omorikae* and *Sitchensis* exhibit two-faced flat leaves with stomatal lines on only one abaxial faces. Conversely subsections *Picea* and *Pungentes* exhibit four-faced leaves with an obtrullate outline in cross section and bear stomatal lines on each of the four faces. *Picea nakauchii* resembles subsections *Picea* and *Pungentes* in these respects. Nine modern species of these two subsections including all species indigenous to Japan are used for comparison with the fossil specimens. This is about one third of all the species in these sections according to Farjon (1990).

*Picea nakauchii* is different from *P. pungens* in subsection *Pungentes* in having a single mass of fibers on the abaxial side of the phloem and in lacking the two-layered hypodermis at only adaxial ridge. In *P. pungens*, a medullary ray divides the mass of phloem

fiber into two parts, and the hypodermis develops two or three layers at both abaxial and adaxial ridges.

Among the examined species of subsection *Picea*, *P. abies*, *P. glehnii*, and *P. torano* are different from *P. nakauchii* in having larger resin canals, 65–140 µm in diameter, encircled by 12–19 epithelial cells instead of the small, 25–35 µm in diameter, with 6–10 epithelial cells in *P. nakauchii*. *Picea torano* and *P. abies* also differ from *P. nakauchii* in having a two-layered hypodermis at both the abaxial and adaxial ridges. *Picea maximowiczii* and *P. alcoquiana* exhibit intermediate-size resin canals, 70–90 µm in diameter with 7–11 epithelial cells, and 50–60 µm in diameter with 8–12 epithelial cells, respectively. *Picea smithiana* closely resembles *P. nakauchii* in having small resin canals, 22–35 µm in diameter, but differs from it in having thick-walled sieve elements.

Among the Japanese species of the genus *Picea*, our fossil leaf resembles *P. koyamai*, and *P. shirasawae* in having similar smaller resin canals. The range in numbers of epithelial cells, phloem fiber, and epithelial cells are similar (Table 2). However, *P. nakauchii* differs from *P. koyamai* and *P. shirasawae* in that the resin canal never becomes larger than 35 µm up to more than 75 µm in the latter. Except for the different size of resin canals, we recognized no morphological difference between *P. nakauchii*, *P. koyamai*, and *P. shirasawae*.

Eight species of compression fossils of the genus *Picea* are known from the Miocene of Japan: *P. hiyamensis* Tanai et Suzuki (1963), *P. kaneharai* Tanai et Onoe (1961), *P. kanoi* Huzioka (1949), *P. koribai* Miki (1948), *P. latibracteata* Miki (1957), *P. magna* MacGinitie (1953), *P. miocenica* Tanai (1961), and *P. ugoana* Huzioka (1949) (Ozaki 1991, Tanai 1961, Tanai and Suzuki 1963, Uemura 1988). Of these, only *P. koribai* is known from a vegetative organ; the other species are described from seeds or seed cones. The leaves of *P. koribai* are acute, 18–22 mm long, 1.7–2.2 mm wide, with stomata on four

Species	Portion of two-layered hypodermis	Diameter of resin canal (µm)	Number of epithelial cells	Number of cells of phloem fiber	Number of cells of endodermis	Diameter of endodermis (µm)
<i>P. nakauchii</i> sp. nov.	abaxial, around resin canal	20–35	6–10	5–15	15–24	260–380
<i>P. abies</i>	abaxial, adaxial	95–105	14–19	5–7	16–18	220–250
<i>P. alcoquiana</i>	abaxial, around resin canal	50–60	8–12	4–7	14–15	230–260
<i>P. glehnii</i>	abaxial	130–140	16–18	4–6	16–18	250–260
<i>P. koyamai</i>	abaxial, around resin canal, (adaxial)*	35–75	6–12	4–16	15–27	220–460
<i>P. maximowiczii</i>	abaxial	70–90	7–11	8–10	14–16	200–240
<i>P. pungens</i>	abaxial, adaxial	65–75	12–14	5–7	22–25	240–250
<i>P. shirasawae</i>	abaxial, around resin canal, (adaxial)*	30–75	8–13	6–13	19–30	270–370
<i>P. smithiana</i>	abaxial, around resin canal	22–35	6–8	6–7	14–15	250–260
<i>P. torano</i>	abaxial, adaxial	65–90	12–13	10–16	20–22	330–420

\*rarely present in thick leaves

faces. *Picea nakauchii* having the leaves of 1.0–2.0 mm wide than that of *P. koribai*. Of the other species, *P. kanoi* resembles *P. koyamai*; *P. kaneharai*, *P. magna*, *P. hiyamensis*, and *P. miocenica* resemble *P. torano*; *P. latibracteata* resembles *P. maximowiczii*, and *P. ugoana* resembles *P. alcoquiana* (Miki 1957, Tanai 1961, Tanai and Suzuki 1963). Since *P. nakauchii* resembles *P. koyamai* and *P. shirasawae*, *Picea kanoi* may be closely related to *P. nakauchii*, but *P. kanoi* is described from a compressed seed and cannot be easily compared with *P. nakauchii*.

Living plants of *P. koyamai* and *P. shirasawae* have a limited distribution in central Japan, while fossils of *P. koyamai* from the glacial Pleistocene show a wider distribution from Shiga to Iwate Prefecture (Miki 1957). *Picea kanoi* is known from the Middle to Late Miocene deposits of Southwest Hokkaido and Northeast Honshu (Huzioka 1949, Tanai and Suzuki 1963, Uemura 1988). In all floras, temperate plant elements such as Juglandaceae, Betulaceae, Fagaceae, and Aceraceae are dominant, and *Picea kanoi* is assigned to a mountain association. The occurrence of *P. nakauchii* in Shimokawa extends the northern distribution of fossil plants comparable with *P. koyamai* and related taxa. It is hoped to investigate the whole Miocene flora in the Shimokawa area.

Reliable records of *Picea* are known from as early as the Oligocene. *P. diettiana* Miller (1970) from Western Montana and *P. eichhornii* Miller (1989) from Washington, USA are described from permineralized cones. They exhibit all the important features of the genus, hence the genus had evolved by the Oligocene (Miller 1970). Considering the features of the cone scale, *P. diettiana* has woody scale apices resembling that of section *Picea*; *P. eichhornii* has papery-thin scale apices similar to those of section *Casicta* (Miller 1989). However, modern species comparative to these Oligocene cones cannot be assigned. On the other hand, the resemblance between *P. wolfei*

Crabtree (1983) from the Miocene of Northwestern Nevada, USA and modern *P. breweriana* of subsection *Omorikae* of section *Picea* has been pointed out (Crabtree 1983). Miocene species from Japan can not be assigned to modern species, but resemble some extant species such as *P. koyamai*, *P. torano*, *P. maximowiczii*, *P. alcoquiana*, all of which are members of subsection *Picea* of section *Picea*. The Miocene fossil record in Japan and the USA indicate that the two subsections of section *Picea* had already diversified by the Miocene. When the fossil records of the genus *Picea* are put together, the genus diverged in the Paleogene, the important characters of the genus had formed and the two modern sections had diverged by the Oligocene, with diversification of section *Picea* occurring in the Miocene. Anatomical study of the petrified leaves from Shimokawa provides a lot of data on the evolution of *Picea*.

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### 松本みどり、大澤毅守、西田 誠：北海道下川層群（中期中新世後期）トウヒ属化石の葉の内部構造と類縁関係

中期中新世後期・下川層群のいわゆる玉ずいには、多数の植物化石が含まれている。この研究ではその中からマツ科トウヒ属の葉に関して、その内部組織を近縁な現生種と比較することにより、系統的類縁関係の推定を行った。日本におけるトウヒ属化石は、これまでに種子及び球果の印象化石や石化材化石を中心に各地から知られているが、石化した葉の内部構造の記載は、日本の第三紀では今回が初めてである。ルベノ沢の化石は保存が極めて良好であり、フッ化水素を用いたピール法により連続切片を作成し内部組織の観察を行った。化石は菱形の横断面を持つこと、篩部纖維が放射柔組織によって二分されないことから、現生のトウヒ属の4亜節（Farjon 1990の分類による）のうちのトウヒ亜節に類似し、その中でも樹脂道が小さいこと、下皮が主に背軸面と樹脂道の回りで2

層になること、内皮の直径や、篩部纖維の細胞の数などの諸特徴から、ヤツガタケトウヒ、ヒメマツハダの2種に最も良く類似する。しかし樹脂道が35  $\mu\text{m}$  以下と極めて小型で大きくならない点が特徴的であり、新種として記載した。今回の報告の化石採集に御案内いただいた、北海道下川町の中内伊勢吉氏にちなんで *Picea nakauchii* sp. nov. と命名した。トウヒ属の化石を世界的に見ると漸新世にはすでに *Picea* 節と *Casicta* 節が分化していたことが示されるがこれらは直接現生種に対比できない。これに対して中新世になると、現生種との類似が明確になり、*Picea* 節の二つの亜節の分化が確認されている。これらの化石の記録から *Picea* 属の分化は古第三紀の初期に起こり、現在の二つの節の分化は漸新世に、さらに中新世には *Picea* 節の多様化が進んだと考えられる。